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A NEW CRYPTIC SPECIES OF SALAMANDER, GENUS *OEDIPINA* (CAUDATA: PLETHODONTIDAE), FROM PREMONTANE ELEVATIONS IN NORTHERN NICARAGUA, WITH COMMENTS ON THE SYSTEMATIC STATUS OF THE NICARAGUAN PARATYPES OF *O. PSEUDOUNIFORMIS* BRAME, 1968

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ABSTRACT. We describe a new species of *Oedipina* (subgenus *Oedipina*) from premontane elevations of three isolated mountains in northern Nicaragua. The new cryptic species differs in molecular characters from its closest relatives: *Oedipina cyclocauda* (an Atlantic lowland species with a distributional range from central Panama to extreme southeastern Nicaragua) and *Oedipina pseudouniformis*. We regard all Nicaraguan specimens previously referred to as *O. pseudouniformis* to be conspecific with the new species herein described and restrict *O. pseudouniformis* as a Costa Rican endemic species. We also record the fourth known locality (and southernmost) of the Nicaraguan endemic *O. nica* and discuss additional species of *Oedipina* that are likely to be found in Nicaragua as field research continues in the country.

RESUMEN. Describimos una nueva especie de *Oedipina* (subgénero *Oedipina*) de alturas premontanas de tres montañas aisladas del norte de Nicaragua. La nueva especie críptica difiere en caracteres moleculares de sus parientes más cercanos: *Oedipina cyclocauda* (una especie de las tierras bajas del Atlántico entre el centro de Panamá y el

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extremo sureste de Nicaragua) y *O. pseudouniformis*. Consideramos a todos los especimenes nicaragüenses previamente referidos como *Oedipina pseudouniformis* representantes de la nueva especie aquí descrita y a *O. pseudouniformis* una especie endémica de Costa Rica. También registramos la cuarta localidad conocida (y más al sur) de la salamandra endémica *O. nica* y discutimos acerca de especies adicionales de *Oedipina* candidatas a ser encontradas en Nicaragua a medida que se continúe investigando en el país.

Key words: 16S; cyt *b*; mtDNA; environmental modeling; *Oedipina koehleri* **sp. nov.**; *Oedipina nica*; Parque Nacional Cerro Saslaya; Reserva Natural Cerro Musún

Despite their remarkably conserved external morphology, Neotropical worm salamanders (Caudata: Plethodontidae: *Oedipina*) have been shown in recent phylogenetic studies to exhibit a surprising degree of evolutionary diversity (García-París and Wake, 2000; McCranie *et al.*, 2008). Most recently, Sunyer *et al.* (2010) described a new species of *Oedipina* of the cryptic subgenus *Oeditriton* (*O. nica*) from three isolated highlands in north-central Nicaragua. The description of *O. nica* marked the first in a series of papers dealing with the systematics of various unresolved populations of *Oedipina* from around the country. The present contribution is the second of these papers and addresses the systematic status of three additional isolated populations of *Oedipina* (two of which had previously been assigned to *Oedipina pseudouniformis*) from northern Nicaragua.

The taxon *O. pseudouniformis* has been reported in Nicaragua from two isolated premontane localities (Brame, 1968; Köhler *et al.*, 2004). In his seminal revision of the genus, Brame (1968) included eight paratypes of *O. pseudouniformis* based on a series collected in July 1957 from "Hacienda La Cumplida, 1.5 km north of Matagalpa, 731 m elevation," Dept. Matagalpa, Nicaragua. Premontane elevations in this area have undergone severe human alteration in the last five decades, and cattle and agriculture (mostly coffee plantations) have isolated the few remaining forest patches to extreme upper portions of the surrounding mountain peaks. Köhler *et al.* (2004) additionally reported two specimens referred to *O. pseudouniformis* from pristine forest between approximately 600 and 945 m elevation in Parque Nacional Cerro Saslaya, Región Autónoma Atlántico Norte, Nicaragua.

Although we have so far failed to secure fresh samples of *Oedipina* from premontane elevations in the surroundings of Hacienda La Cumplida in Matagalpa, we recently collected an additional specimen from premontane elevations at Parque Nacional Cerro Saslaya, as well as two specimens of *Oedipina* from Reserva Natural Cerro Musún, Dept. Matagalpa, Nicaragua. Although external morphology has been unhelpful in elucidating taxonomic assignments for these populations, phylogenetic analysis of data from two mitochondrial genes (cytochrome *b* [cyt *b*] and 16S) demonstrates that the Saslaya and Musún populations represent a single undescribed species in the subgenus *Oedipina*, a sister of a clade of Costa Rican taxa *Oedipina cyclocauda* and *O. pseudouniformis*. We herein provide a taxonomic description of this new species, evaluate its phylogenetic relationships within the genus *Oedipina*, and further comment on our understanding of Nicaraguan populations of *Oedipina*.

MATERIAL AND METHODS

Taxon Sampling. We formulated a new phylogenetic hypothesis for the genus *Oedipina*, and included representatives of both the Saslaya and Musún populations of the new species, as well as all congeners available

TABLE 1. LOCALITY, VOUCHER, AND GENBANK ACCESSION NUMBERS FOR TAXA AND SAMPLES USED IN PHYLOGENETIC ANALYSES.

Taxon	Locality	Voucher	16S	Cyt *b*
Nototriton barbouri	Honduras: Atlántida	UF 156538	GU971733	GU971734
Oedipina alleni	Costa Rica: Puntarenas	MVZ 190857	AF199207	AF199149
Oedipina carablanca	Costa Rica: Limón	No voucher	FJ196862	FJ196869
Oedipina collaris	Panamá: Coclé	SIUC H 8896	FJ196863	FJ196870
Oedipina complex	Panamá: Colón	MVZ 236255	AF199213	AF199157
Oedipina cyclocauda	Costa Rica: Heredia	MVZ 138916	AF199214	AF199158
		MVZ 203747	AF199215	AF199159
Oedipina elongata	Guatemala: Izabal	UTA A-51906	AF199216	AF199160
Oedipina gephyra	Honduras: Yoro	UF [JHT2443]	JN190930	JN190936
Oedipina gracilis	Costa Rica: Heredia	MVZ 210398	AF 199219	—
Oedipina grandis	Costa Rica: Puntarenas	MVZ 225904	FJ196864	AF199164
Oedipina ignea	Honduras: Ocotepeque	USNM 530586	AF199231	AF199192
Oedipina kasios	Honduras: Olancho	MVZ 232825	FJ196866	FJ196872
	Honduras: Francisco Morazán	UF 156500	HM113477	HM113484
Oedipina koehleri	Nicaragua: Atlántico Norte	UF 156456	JN190926	JN190933
sp. nov.	Nicaragua: Matagalpa	SMF 90079	JN190927	JN190934
Oedipina leptopoda	Honduras: Yoro	MVZ 167772	—	AF199193
Oedipina maritima	Panamá: Bocas del Toro	MVZ 219997	AF199221	AF199166
Oedipina nica	Nicaragua: Matagalpa	MHUL 003	JN190928	—
	Nicaragua: Jinotega	MVZ 263774	HM068306	HM068303
		UF 156447	HM113474	HM113482
		UF 156453	HM113475	HM113483
Oedipina pacificensis	Costa Rica: Puntarenas	UCR 12063	AF199222	AF199169
Oedipina petiola	Honduras: Atlántida	USNM 343462	AF199217	AF199161
Oedipina poelzi	Costa Rica: Alajuela	MVZ 181235	—	AF199172
		MVZ 206398	AF199223	AF199171
Oedipina	Costa Rica: Cartago	MVZ 203749	AF199227	AF199178
pseudouniformis		MVZ 181229	—	AF199179
		MVZ 190852	—	AF199177
Oedipina quadra	Honduras: Gracias a Dios	MCZ 232824	FJ196865	FJ196871
Oedipina savagei	Costa Rica: Puntarenas	UCR 14587	AF199209	AF199152
Oedipina sp. 1	Nicaragua: Jinotega	SMF 78738	FJ196868	—
Oedipina stenopodia	Guatemala: San Marcos	MVZ 163649	AF199228	AF199181
Oedipina taylori	Guatemala: Zacapa	USAC 1134	HM068304	HM068302
Oedipina tomasi	Honduras: Cortés	UF 150066	JN190929	JN190935
Oedipina uniformis	Costa Rica: Cartago	MVZ 203751	AF199230	AF199190

on GenBank (http://www.ncbi.nlm.nih.gov); species, locality, and voucher information for these taxa are summarized in Table 1. Acronyms for museum collections follow those of Leviton *et al.* (1985), except MHUL (Museo Herpetológico de la UNAN–León, Universidad Nacional Autónoma de Nicaragua–León, León, Nicaragua), N field numbers, which correspond to specimens collected in Nicaragua between 2007 and 2008 by University of Florida field teams in collaboration with the UNAN–León, and JHT (field series of the second author), which is used for a specimen of *Oedipina gephyra* donated to the University of Florida (UF) in May 2009 that remains uncataloged. *Nototriton barbouri*, a member of the sister genus to *Oedipina* (García-París and Wake, 2000; Wiens *et al.*, 2007), was used as an outgroup.

Morphological Examinations. Measurements follow those used in McCranie *et al.* (2008). All measurements are in millimeters (mm) and made to the nearest 0.1 mm with dial calipers and a dissecting microscope with ocular micrometer. SL is the distance from the tip of the snout to the posterior angle of the vent. Males were determined by the presence of mental glands behind the tip of the mandible and small papillae in the anterior part of the vent and females by the presence of folded vent margins and absence of mental glands and vent papillae. Maxillary and vomerine tooth counts are totals of the paired bones. Limb interval equals the number of costal interspaces between adpressed limbs. We provide a list of the Nicaraguan comparative specimens examined in the Appendix.

DNA Extraction and Sequencing. Template DNA was extracted from tissue with a Qiagen PureGene DNA Isolation Kit (Qiagen, Valencia, California) following manufacturer's instructions. Fragments of two mitochondrial genes were targeted for amplification: a 516-bp fragment of the 16S large subunit rRNA (16S) was amplified using primers 16Sar-L and 16Sbr-H (Palumbi *et al.*, 1991), and a 692-bp fragment of cyt *b* was amplified using primers MVZ15 and MVZ16 (Moritz *et al.*, 1992). Conditions for PCR did not differ between genes, with initial denaturation at 94°C for 3 min, 35 amplification cycles of 45 s denaturation at 94°C, 45 s annealing at 50°C, 45 s extension at 72°C, and a final extension of 5 min at 72°C. Samples were cleansed of unincorporated dNTPs through application of USB ExoSAP-IT before following standard sequencing protocol on an ABI 3130xl automated sequencer (Applied Biosystems, Foster City, California) at the University of Florida WEC/SFRC Molecular Ecology Lab.

Phylogenetic Analyses. Cytochrome *b* sequences were trimmed to 385 bp to match available sequences in GenBank from other studies (García-París *et al.*, 2000; McCranie *et al.*, 2008; Sunyer *et al.*, 2010), and sequence alignment was estimated using MAFFT (Katoh *et al.*, 2002). Bayesian phylogenetic analysis was performed in MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001), with sequence data partitioned by gene for 16S and by codon position for cyt *b*. Using the Akaike Information Criterion in MrModeltest2.2 (Nylander, 2004), we selected the nucleotide substitution model GTR+I+Γ for 16S, and GTR+I+Γ, GTR+Γ, and HKY+Γ for first, second, and third codon position of cyt *b*, respectively. Bayesian analysis consisted of two parallel runs of four chains, run for 20×10^6 generations and sampled every 1,000 generations, with the first 4,000 samples discarded as burn-in. The remaining 16,001 post–burn-in trees from both runs were used to generate a 50% majority rule consensus tree. Cumulative and sliding window plots of split frequencies and the correlation of split frequencies in first versus second runs were visualized in Geneious v4.8 (Drummond *et al.*, 2009) to assess convergence around posterior quantities. Maximum likelihood (ML) phylogenetic analysis was conducted in RAxML v7.2.6 (Stamatakis, 2006) using the same data partitions as the Bayesian analysis and the GTR+Γ model for each partition; 1,000 bootstrap replicates were performed using the rapid bootstrapping algorithm.

Macroecological Modeling. We created an environmental niche model based on the localities of *Oedipina koehleri* using the maximum entropy method (Phillips *et al.*, 2006) as implemented in the program MaxEnt, to determine whether a resulting distribution model would predict occurrence of *O. koehleri* at Hacienda La Cumplida, Dept. Matagalpa, the locality given for eight paratypes of *O. pseudouniformis* (Brame, 1968). Using presence-only data (i.e., local-

ities of occurrence), MaxEnt uses the principle of maximum entropy density estimation to generate a probability distribution (Phillips *et al.*, 2006; Phillips and Dudík, 2008). It has been shown to produce more accurate models with lower sample sizes than other niche-modeling methods (Elith *et al.*, 2006; Hernandez *et al.*, 2006). We used the 19 WorldClim Current BioClim climate layers, which have a resolution of 30 arc-seconds (about 1 km^2). These layers are based on data from 1950 to 2000 and include variables reflecting annual, as well as seasonal, climatic trends and extremes of precipitation and temperature (Hijmans *et al.*, 2005). We did not make any assumptions of correlation among these variables and thus chose to use the entire set of environmental layers. We clipped the WorldClim layers in ESRI ArcGIS 9.3 to our working extent before using them in MaxEnt. A model representing the probability of occurrence of *O. koehleri* was produced in MaxEnt using a cross-validation approach for our specimen localities. The cross-validation function splits the data set into *n* samples of one case that are individually tested against all remaining samples, which become the training set of localities during each run (Araújo *et al.*, 2005). This eliminated the need to partition a data set into large training and testing sets. In this case, this approach was necessary because splitting the data would have resulted in a training set of insufficient size. The final mean logistic output of the model runs was used to assess our results. The area under the curve (AUC) of the receiver operating characteristic plot was used to evaluate model performance.

Systematic Account

Oedipina **koehleri** *sp. nov.*

Figure 1

Oedipina pseudouniformis (Brame, 1968) in part: Brame (1968:25–28, fig. 20). Paratypes UMMZ 119523(1–8) from "Hacienda La Cumplida, 1.5 km N of Matagalpa, elevation 731 m (2,400 ft), Dept. Matagalpa, Nicaragua"; Villa (1972:51–54); Villa (1983:21); Villa *et al.* (1988:7–8); Köhler (1999:11); Köhler (2001:23); Ruiz and Buitrago (2003:36–37); Köhler *et al.* (2004:18); Sunyer and Köhler (2010:500); Köhler (2011:86).

Holotype. UF 156456, an adult male, from Parque Nacional Cerro Saslaya (along the trail from "Las Guardiolas" to "El Revenido"), 13°42.8′N, 85°01.9′W, 724 m above sea level (a.s.l.), Región Autónoma Atlántico Norte, Nicaragua, collected 1 August 2008 by Scott L. Travers, Stephen Doucette-Riise, Sergio C. González, Atanasio Baldonado, and Ignacio Cruz (original field number N614).

Paratypes. Four; SMF 82225, an adult male, from the southern slope of Parque Nacional Cerro Saslaya (along the trail from Campamento "Las Pavas" [13°44.5′N, 85°01.5′W] to Campamento "Los Monos" [13°45.1′N, 85°02.2′W]), 945 m a.s.l., Región Autónoma Atlántico Norte, Nicaragua; SMF 82874, an unsexed juvenile, from the southern slope of Parque Nacional Cerro Saslaya (along the trail from Campamento "El Carao" [13°42.8′N, 84°58.7′W] to Campamento "Las Pavas" [13°44.5′N, 85°01.5′W]), 400–600 m a.s.l., Región Autónoma Atlántico Norte, Nicaragua; SMF 90078–79, both adult females, from the southern slope of Reserva Natural Cerro Musún (FUNDENIC Cabins [12°57.3′N, 85°13.9′W]), 628 m a.s.l., Dept. Matagalpa, Nicaragua.

Referred Specimens. Eight; UMMZ 119523, four adult males and four adult females, all from Hacienda La Cumplida, 1.5 km N of Matagalpa, 731 m a.s.l., Dept. Matagalpa, Nicaragua.

Diagnosis. A slender species of moderate size (largest referred specimen 50.4 mm SL) and robustness assigned to the genus *Oedi-*

Figure 1. Adult female paratypes of *Oedipina koehleri* (a) SMF 90078 and (b) SMF 90079 from Reserva Natural Cerro Musún; and (c) juvenile paratype of *O. koehleri* (SMF 82874) from Parque Nacional Cerro Saslaya.

pina based on the presence of more than 13 costal grooves between the short limbs, and tail much longer than head plus body. This species is a member of the subgenus *Oedipina* (based on molecular data; Fig. 2) and is distinguished from its closest relatives, *O. pseudouniformis,* in having fewer maxillary teeth (mean 38 vs. 49.8 in males; 39.8 vs. 45 in females) and vomerine teeth (mean 20.5 vs. 25.9 in males; 22.2 vs. 25.7 in females), and *O. cyclocauda* in having a more rounded snout, a broader head, and somewhat longer

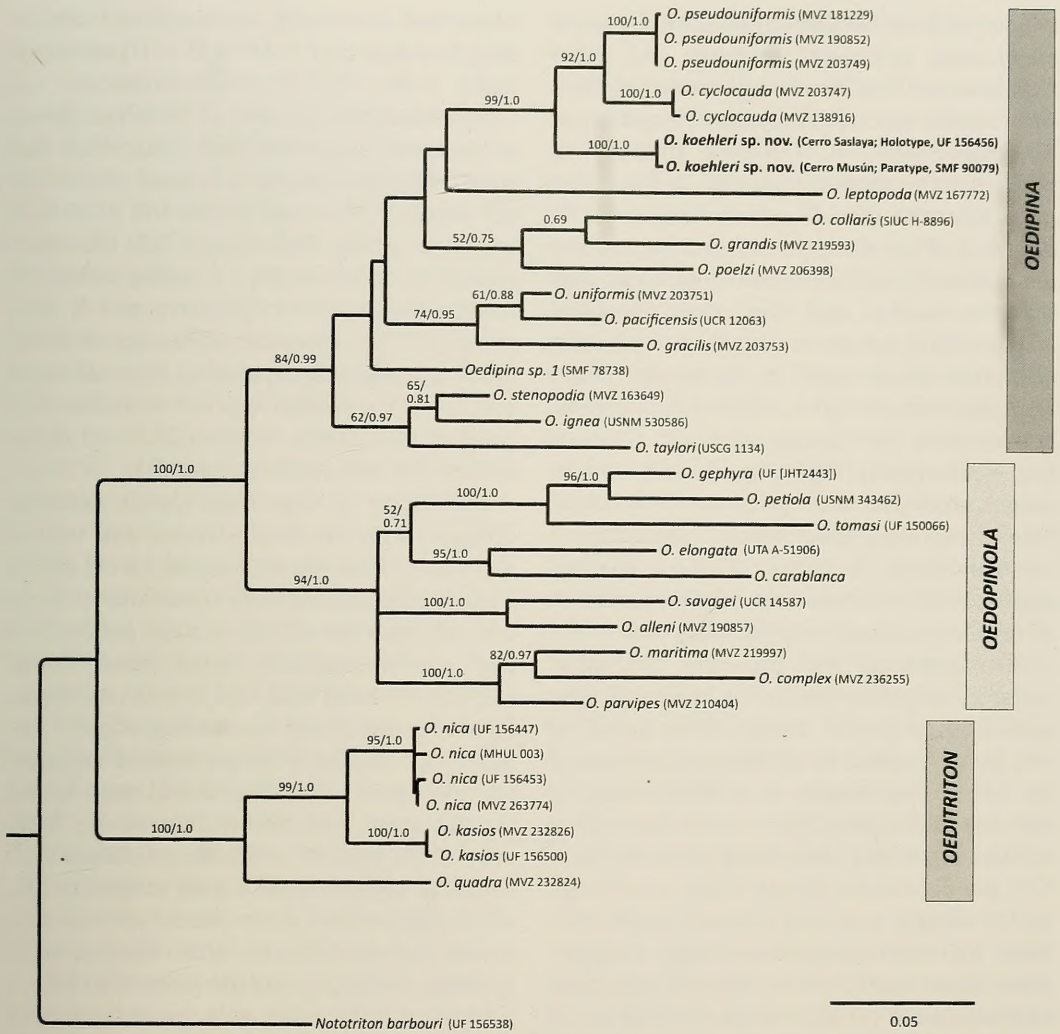

Figure 2. Maximum likelihood (ML) phylogram (lnL = −5,504.696063) of the genus *Oedipina*, showing placement of *Oedipina koehleri* (shown in bold) within the *Oedipina* subgenus. Bootstrap support values from ML analysis (scaled 0–100) and Bayesian posterior probabilities (scaled 0–1.0) are shown above the branches; ML bootstrap values omitted when less than 50, posterior probabilities omitted when less than 0.65.

legs. Further distinguished from its closest geographic congener, *O.* (*Oeditriton*) *nica*, in having pale brown pigmentation on the proximal limb surfaces, in being slightly more robust, in having fewer maxillary teeth, and in having shorter limbs (hind limb length has mean value of 7.28 times SL in males, 7.36 in females, averaging 11.3 costal folds uncovered by adpressed limbs (limb interval) vs. hind limbs more than 8 times SL and limb interval more than 13 in *O. nica*). The only other Nicaraguan species of the genus, *Oedipina collaris*, is much larger and has a long pointed snout and large limbs, manus, and pes. The new species differs from other members of its clade as follows: it is more

robust and has longer limbs than *Oedipina pacificensis, uniformis, leptopoda,* and *gracilis*; it is much smaller and lacks a dorsal band of brownish color dorsally that characterizes *Oedipina poelzi* and *Oedipina altura*; it is much smaller than *O. grandis*; it has more maxillary teeth than *O. paucicarinatus* and *O. alfaroi*; it is less elongate with more maxillary teeth than *O. taylori*; it has longer legs with broader manus and pes than *Oedipina stenopodia*; it has fewer maxillary teeth than *Oedipina ignea*; and it is smaller than *Oedipina stuarti.* It differs also by its combination of having distinct, rounded but syndactylous digits, moderately broad manus and pes, and predominantly black coloration, with some brown pigmentation on the dorsal surfaces of the proximal segments of the limbs and dispersed whitish to bluish speckling over the body and tail.

Description of the Holotype. An adult male, as judged by having an inconspicuous mental gland behind the tip of the mandible and small papillae in the anterior portion of the vent. This species is a moderate-sized member of the genus (SL = 40.4 mm) with a moderately broad head (head width 10.9% of SL), slender habitus (trunk width at midbody 12.1% of SL), and long tail (tail length 1.82 times SL) with no apparent basal constriction; nares small, snout broadly rounded, and nasolabial protuberances not well developed; maxillary teeth 17 on left side and 20 on right side (37 total maxillary teeth), single premaxillary tooth set relatively far forward of interior margin of upper lip; vomerine teeth arranged in two arches with seven teeth on left arch and five teeth on right arch (12 total vomerine teeth); costal grooves number 19 and are relatively shallow, but well demarcated by unpigmented line at deepest point of groove; limbs short, 13 costal grooves visible between adpressed limbs; front and hind feet with rounded, differentiated toe tips, toes well-defined but fused and essentially syndactylous; relative length of digits is I < IV < II < III on hands and I < V < II < IV < III on feet.

Measurements (in mm) of Holotype. Snout to posterior angle of vent (SL) 40.4; tail width 4.9; head length 6.7; head width 4.4; tail length 73.6; trunk width 4.9; hind limb length 6.2; front limb length 5.2; hind foot width 1.2; eyelid length 1.7; eyelid width 0.9; interorbital distance 1.6; anterior rim of orbit to snout 1.6; distance separating internal nares 1.0; distance separating external nares 1.8; snout projection beyond mandible 0.3; distance from axilla to groin 28.9; tail depth at base 3.4; tail width at base 3.4.

Coloration of the Holotype in Alcohol. Ground color of dorsal, lateral, and ventral surfaces of head, body, and tail black; dorsal surface of head and ventral surfaces of body and tail, and tip of tail, slightly paler. Chin and throat markedly paler than dorsal surfaces of head and body, with an unpigmented band along the leading edge of the gular fold. The proximal portions of the limbs are also paler than the dorsal and lateral ground color, and the surface of the body around the point of articulation for each limb is pale to unpigmented. Under magnification, all dorsal surfaces are profusely spotted with brown chromatophores, which become more numerous ventrally and are most abundant in the midventral portion of the posterior half of the body. The midlateral portions of the body are paler and the ventral surfaces are mostly unpigmented, with some scattered silvery spots present on the throat and anterior portions of the ventral surface. Pale chromatophores so profuse on chin that ground color is not apparent, giving the chin an overall pale appearance. The upper lip and nasolabial protuberances are unpigmented. The center of each costal groove is unpigmented, making the grooves appear more pronounced than would be evident from their actual physical depth.

Variation. Variation in external morphology among the four adult specimens in the type series is minimal. The adult male paratype (SMF 82225) is larger than the male holotype (UF 156456) and proportionally has the longest tail, measuring 48.0 mm SL with a tail length 2.4 times that of SL; it has 39 (18/21) maxillary teeth, a single premaxillary tooth, and 19 (9/10) vomerine teeth. Compared with the holotype, SMF 82225 has a slightly broader head (head width/SL = 0.116 vs. 0.109), shorter forelimbs (right forelimb length/SL = 0.116 vs. 0.121) and hind limbs (right hind limb length/SL = 0.137 vs. 0.153), and wider hind feet (right hind foot width/SL = 0.035 vs. 0.030). Two adult female paratypes (SMF 90078–79) are larger than the holotype; SMF 90078 is the longest bodied type specimen of *O. koehleri* (49.2 mm SL, tail length 1.74 times SL), and has 40 (19/21) maxillary, four premaxillary, and 19 (10/9) vomerine teeth; SMF 90079 measures 44.6 mm SL with a tail length 1.62 times that of SL. Compared with the holotype, the two female paratypes have slightly narrower heads (head width/SL = 0.104–0.105 vs. 0.109), shorter forelimbs (right forelimb length/SL = 0.096–0.101 vs. 0.121), and shorter hind limbs (right hind limb length/SL = 0.120–0.126 vs. 0.153).

The referred specimens (UMMZ 119523; eight specimens) also show little variation from the type series. One specimen, a female, is the largest representative of *O. koehleri*, measuring 50.4 mm SL with a tail that is 1.8 times that of the SL. The remaining seven specimens in this series range from 39.3 to 42.9 mm SL in males (with tails 1.5–1.7 times SL) and 40.7 to 44.6 mm SL in females (with tails 1.6–1.7 times SL). Compared with the type series, the UMMZ series has a similar number of maxillary teeth (36–39 in four males, 36–44 in females) and a slightly higher count of vomerine teeth (20–22 in four males, 23–26 in females) but otherwise agrees with the morphological proportions of the type series.

Phylogenetic Relationships. Our analyses support assignment of the populations at Saslaya and Musún to a single taxon, *O. koehleri* (Fig. 2, ML bootstrap value = 100, posterior probability = 1.0), and also support a sister relationship between *O. koehleri* and the more southerly *O. cyclocauda*/*O. pseudouniformis* clade (Fig. 2, ML bootstrap value = 99, posterior probability = 1.0) within the subgenus *Oedipina*. Deeper relationships within the subgenus *Oedipina* are generally poorly resolved, with four clades: an *O. collaris*/*O. grandis*/*O. poelzi* clade, an *O. gracilis*/*O. pacificensis*/*O. uniformis* clade, an *O. ignea*/*O. stenopodia*/*O. taylori* clade, and the aforementioned *O. cyclocauda*/*O. pseudouniformis*/*O. koehleri* clade. Additionally, the relationships of two taxa with respect to the rest of the subgenus *Oedipina* are unresolved, *O. leptopoda* and *Oedipina* sp. 1 (see comments in Sunyer *et al.* [2010] regarding *Oedipina* sp. 1). Monophyly of the subgenus *Oedipina* is supported (84/0.99), as is the sister taxon relationship between the subgenera *Oedipina* and *Oedopinola* (100/1.0).

Natural History. This is a secretive and fossorial species known to occur from approximately 600 to 945 m elevation at three isolated localities in northern Nicaragua (Fig. 3). Two of these localities (Cerro Saslaya and Cerro Musún) correspond to the Premontane Wet Forest formation and the remaining locality (near Matagalpa) to the Premontane Moist Forest formation (Holdridge, 1967). The holotype was collected in undisturbed, primary broadleaf rainforest with a dense canopy structure and a relatively open understory. It was found under a fallen log during a late-morning hike while ascending the southern slopes of Cerro El Toro, a sister peak approximately 5 km southwest of Cerro Saslaya that lies within

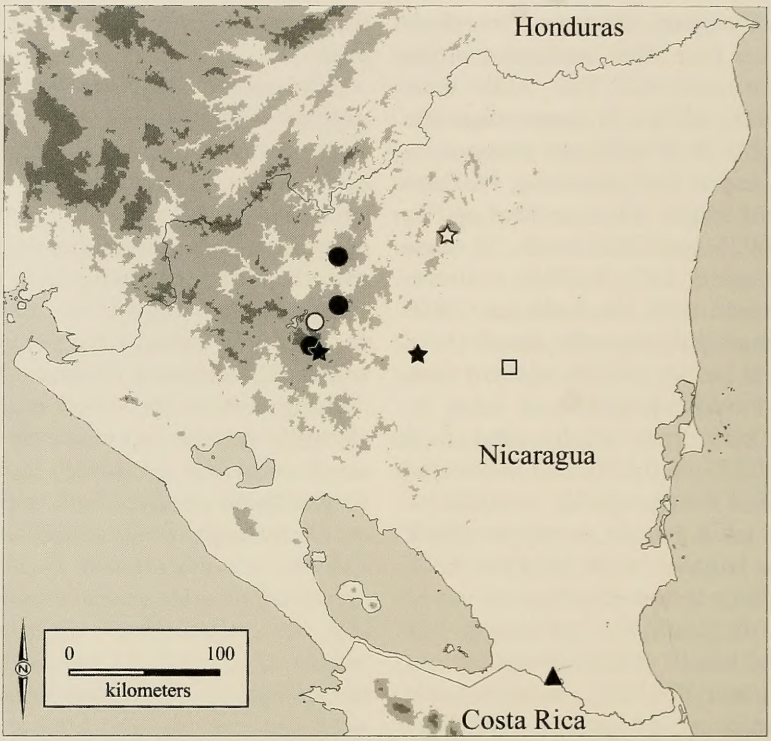

Figure 3. Map of Nicaragua showing the localities of members of the genus *Oedipina* (see Appendix): *O. koehleri* (stars),-*O. nica* (circles), *O. collaris* (square), and *O. cyclocauda* (triangle). Open symbols represents each species' type locality, if it appears on map. If situated very close to one other, we combined distribution points to yield a single point on our map. Water surfaces are shaded pale gray. Areas above 600 m are shaded gray. Areas above 1,200 m are shaded dark gray.

the confines of the park boundaries. The adult male paratype from Parque Nacional Cerro Saslaya (SMF 82225) was collected around 1400 h in pristine forest under a decaying log alongside a forest trail on a moderately steep hill slope. It suddenly jumped downslope by body flipping. The juvenile paratype (SMF 82874) from Parque Nacional Cerro Saslaya was collected around 0900 h in pristine forest under a large rock at the edge of a shady stream bank. It was found buried in a wet mixture of mud-rich sand and debris. The paratypes from Reserva Natural Cerro Musún (SMF 90078–79) were collected in the garden of an isolated tourist cabin, which, although surrounded by pastureland, is relatively close to the reserve's forest edge. They were both found during diurnal surveys involving close inspection of large piles of a humid mixture of mostly cut grass with some leaf litter and other groundskeeping debris from the garden, characterized by a few large trees that gave partial shade to the grass and ornamental bushes. A third specimen escaped by quickly burrowing itself into the dense compost.

Macroecological Modeling. Our environmental niche model appeared to track the niche requirements and distribution of *O. koehleri* accurately because the resulting mean AUC value of our test runs was 0.984

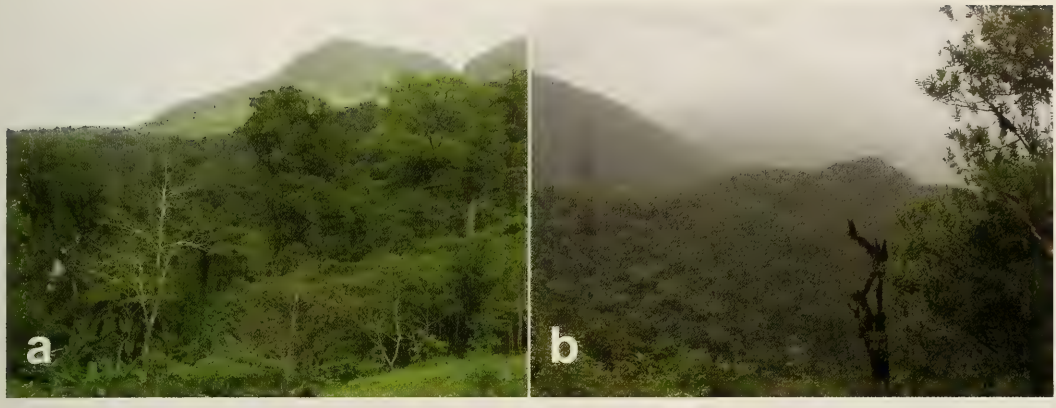

Figure 4. Habitat of *Oedipina koehleri* from (a) Reserva Natural Cerro Musún and (b) Parque Nacional Cerro Saslaya.

(SD = 0.011), where a value of 1 is optimal and 0.5 is as good as random. This interpretation of our AUC value is consistent with the literature for other taxa (Fielding and Bell, 1997; Osborne and Suarez-Seone, 2002; Hernandez *et al.*, 2006; Rödder *et al.*, 2010). On comparing the model's predictions with the Hacienda La Cumplida locality (Fig. 4), we see that our environmental niche modeling predicts a high probability of occurrence for *O. koehleri* at and around that locality, as well as throughout the premontane areas of northern Nicaragua. Thus, the locality Hacienda La Cumplida resides within an area where the environmental conditions are nearly optimal for the presence of *O. koehleri*, further supporting inclusion of the Nicaraguan paratypes of *O. pseudouniformis* under the new taxon.

Etymology. The specific name *koehleri* is a patronym for our friend and colleague Gunther Köhler, in recognition of his many important contributions to the herpetology of Central America in general and Nicaragua in particular.

Conservation Status. Using the criteria established by IUCN for evaluating threatened species, *O. koehleri* should be classified as Endangered (EN B2ab[iii]) because of its limited distribution (known only from three isolated mountainous forest areas with a total extent of less than 500 km^2) and the continued loss of habitat at these localities. Despite repeated searches, representatives of this species in the vicinity of Brame's (1968) Matagalpa locality have not been collected since 1957, and the locality is almost completely converted to agriculture, cattle ranching, or otherwise degraded, as is the majority of intervening territory for the two localities of the type specimens.

DISCUSSION

Members of the subgenus *Oedipina* are noted for their lack of morphological differentiation (Taylor, 1952; Brame, 1968; Good and Wake, 1997; García-París and Wake, 2000), which has led to a somewhat confusing taxonomic history for some populations. Phylogenetic analysis of two mitochondrial loci indicate that *O. koehleri* is the sister species to the clade containing *O. pseudouniformis* and *O. cyclocauda* (Fig. 2), two morphologically unremarkable species described on the basis of Costa Rican material. Good and Wake (1997) commented on the difficulty of distinguishing *O. pseudouniformis* and *O. cyclocauda* from one another on

morphological grounds, and the same is true for *O. koehleri*. However, all three species are genetically well differentiated (Fig. 2) and are not known to occur in sympatry, supporting the validity of each taxon (Savage, 2002).

The type locality of *O. pseudouniformis* is near Turrialba, Prov. Cartago, Costa Rica, and the original description of this species included 182 paratypes (Brame, 1968). All of these paratypes were collected in the lowlands and premontane elevations of Costa Rica, with the exception of eight specimens collected at premontane elevations in Dept. Matagalpa, Nicaragua (Brame, 1968). Paratypes from Nicaragua average fewer maxillary teeth than Costa Rican *O. pseudouniformis* but otherwise are indistinguishable from the Costa Rican specimens (Brame, 1968). Counts of maxillary teeth can be useful in discriminating species of *Oedipina* (Brame, 1968). Some species lack teeth entirely, whereas those of *O. pseudouniformis* and *O. koehleri* are moderately high in number and not very useful for diagnostic purposes. Savage (2002:156) did not include Nicaragua in the distribution of *O. pseudouniformis* and only briefly mentioned the Nicaraguan population assigned to that species (Savage, 2002:150). Given that the Matagalpan and Costa Rican populations are isolated by the Nicaraguan Depression, one of the major biogeographic boundaries in Central America (Savage, 2002), and that most species of the genus *Oedipina*, other than a few lowland species, have relatively restricted distributions (AmphibiaWeb, 2011), we think it likely this Matagalpan population represents a different taxon than *O. pseudouniformis*. Although we lack fresh tissue samples for molecular analysis from the Matagalpan population, we refer the Nicaraguan paratypes of *O. pseudouniformis* to *O. koehleri* (as referred specimens) on the basis of evidence from morphological characteristics and macroecological modeling (see Fig. 5). Therefore, *O. pseudouniformis* is no longer considered to occur in Nicaragua, and its distribution is restricted to Costa Rica.

The predicted distribution of *O. koehleri* corresponds to the premontane slopes of the southern terminus of the nuclear Central American highlands, along the humid Atlantic versant (Fig. 5). This area is relatively poorly known in terms of its herpetological diversity and includes a relatively vast portion of land extending from Departamento Chontales in central Nicaragua to the northern border of the country, and potentially extending peripherally into southeastern Honduras. Unfortunately, premontane elevations within this area are highly disturbed and have largely been converted to agriculture or other anthropogenic uses, with few exceptions. Intact premontane habitat within the predicted distribution of *O. koehleri* appears to be limited to the few mountains present in the large Reserva de la Biosfera Bosawas and a series of relatively small protected areas, which include both localities of the type specimens as well as the following Reservas Naturales: Cerro Apante, Cerro Banacruz, Cerro Cola Blanca, Cerro Cumaica-Cerro Alegre, Cerro Datanlí-El Diablo, Cerro Guabule, Cerro Kilambé, Cerro Kuskawas, Cerro Mombachito-La Vieja, Fila Cerro Frío-La Cumplida, Fila Masigüe, Macizo de Peñas Blancas, Sierra Amerrisque, Sierra Quirragua, and Cerro El Arenal. Recent field trips to the highlands of the vicinity of Reserva Natural Cerro El Arenal (in Finca Monimbó, the property adjacent to Hacienda La Cumplida, where the Nicaraguan paratypes of *O. pseudouniformis* were collected) resulted in the addition of a single specimen of *O. nica* (MHUL 003), which corresponds to the fourth known population and southernmost distribution record of this Nicaraguan en-

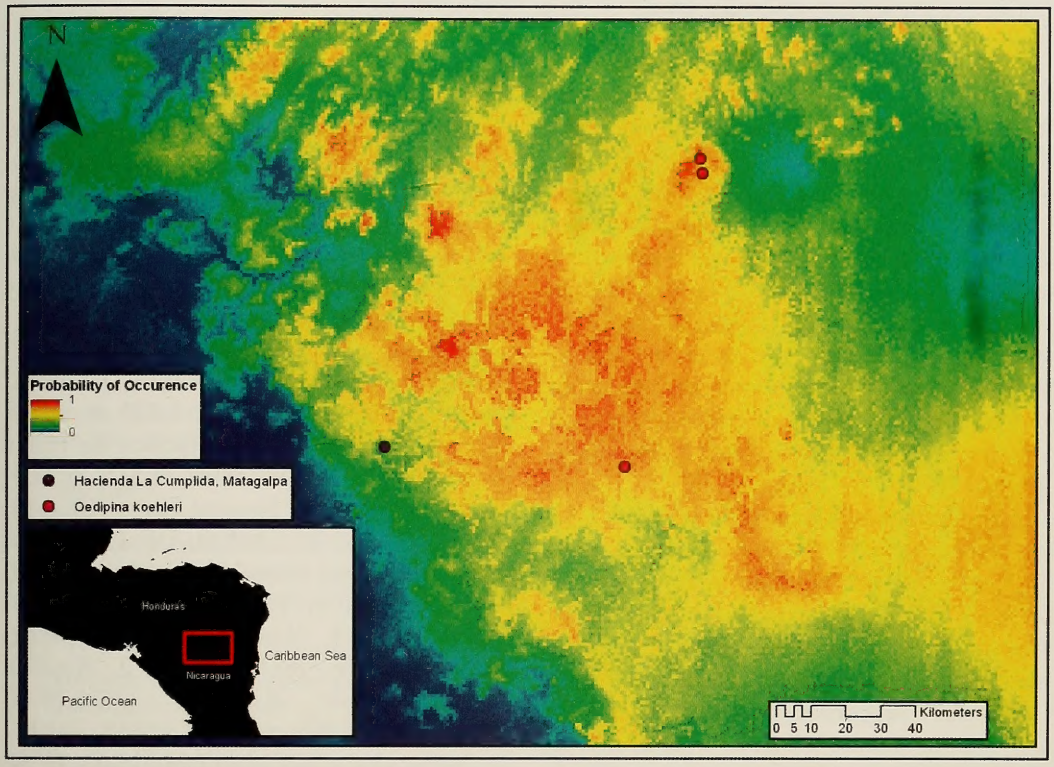

Figure 5. Environmental niche modeling showing the potential distribution of *Oedipina koehleri* in northern Nicaragua.

demic species (see Figs. 2 and 3, Table 1, and Appendix).

Oedipina koehleri is the fourth species of worm salamander recorded in Nicaragua (see Fig. 3), and more species of this genus are likely to be encountered as systematic investigation continues in the country. Aside from known Nicaraguan specimens with ambiguous taxonomic assignments (see Sunyer *et al.*, 2010), at least three more species of *Oedipina* have been recorded from relatively near the political border in neighboring Honduras and Costa Rica and are likely to be found in Nicaragua as field research continues in the country: *O. quadra* is known from the lowland Caribbean slope of northern and eastern Honduras approximately 5 km from the border between Honduras and Nicaragua (McCranie *et al.*, 2008) in habitat continuous with that of adjacent Nicaragua and likely occurs in broadleaf rainforests in the northeastern part of the country; *O. taylori* occurs at low and moderate elevations on the Pacific versant from southeastern Guatemala to southern Honduras (McCranie and Wilson, 2002) in similar habitat as that in northwestern Nicaragua and could occur in premontane forests in that area; and *O. gracilis* is known from the humid Atlantic lowlands between extreme northwestern Panama and northeastern Costa Rica (Savage, 2002) in habitat continuous with that in nearby southeastern Nicaragua and could occur in the Río San Juan rainforests.

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APPENDIX

Specimens Examined

Oedipina collaris. Nicaragua: *Atlántico Sur*: Topaz Mine, 90 miles NW of Bluefields and 50 miles back in direct line from the coast, 120 m: USNM 37350.

Oedipina cyclocauda. Nicaragua: *Río San Juan*: Finca El Tamagás, approximately 1.5 km south of El Castillo: KU 173532.

Oedipina nica. Nicaragua: *Jinotega*: El Gobiado, Reserva Natural Cerro Datanlí-El Diablo, 13°09′N, 85°52′W, 1,420 m: MVZ 263774; Reserva Natural Macizos de Peñas Blancas, 13°17′N, 85°43′W, 1,515 m: UF 156453–55; Reserva Natural Cerro Kilambé, 13°34′N, 85°42′W, 1,625 m: UF 156443–45; Reserva Natural Cerro Kilambé, 13°35′N, 85°43′W, 1,660 m: UF 156446–50; Camp El Hielo, Reserva Natural Cerro Kilambé, 1,490 m: SMF 78736; Camp 2, Reserva Natural Cerro Kilambé, 13°35.25′N, 85°41.50′W, 1,360 m: SMF 78737, 78739–40; *Matagalpa*: Finca Monimbó, 13.03173°N, 85.88682°W, 1,360 m: MHUL 003.

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